Ecological Systems*

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January 18, 2008

Article Outline

*invited contribution for the *Encyclopedia of Complexity and System Science*

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Glossary

- **Food Webs**

  Networks depicting who eats whom in an ecological community.

- **Compartments**

  Groups of highly interacting nodes with few connections to nodes from other groups.

- **Scale-free Networks**

  Very heterogeneous networks in which the bulk of nodes have a few links but a few nodes have a very large number of links.

- **Mutualistic Networks**

  Two-mode networks depicting the mutually beneficial interactions between plants and their pollinators or seed dispersers.

- **Connectivity Correlation**

  A measure of network structure that represents the correlation between the number of interactions of a node and the average number of interac-

tions of the nodes it interacts with. A negative connectivity correlation would represent a modular network.

- **Species Strength**

  A measure of the importance of a species in terms of the total weight of its connections.

- **Network Motifs**

  Patterns of interconnections significantly over-represented in complex networks. These may be regarded as the simple building blocks of complex networks.

- **Trophic Cascades**

  Changes in population abundance that propagate through more than one trophic link in the food chain.

- **Ecosystem Shifts**

  Sudden qualitative changes in the state of an ecosystem (i.e., from clear to turbid waters in a lake) following a continuous tuning of a variable such as nutrient load.

- **Deterministic Chaos**

  Aperiodic, random-like time series generated by low dimensional, non-linear, deterministic models.

- **Lyapunov Exponent**

  A measure of the degree of divergence of initially close trajectories in the phase space that is characteristic of deterministic chaos.

- **Coupled Map Lattice**

  Dynamical system with discrete time, discrete space, and continuous state. It was first used by the physicist Kunihiko Kaneko in relation to spatiotemporal chaos and later on used in ecology as a model of spatiotemporal systems.

- **Interacting Particle System**

  Stochastic spatial models with discrete time, discrete space, and finite states. They have been used as spatially extended models of populations and epidemics, and have been widely analyzed by Richard Durrett and Simon Levin.

- **Metapopulation**

  A population of populations maintained in a dynamical balance between local extinctions and recolonizations from nearby local populations.

- **Extinction thresholds**

  Critical values in the amount of habitat destroyed at which a metapopulation goes extinct.

1 Definition of the Subject and its Importance

Ecological systems are paradigmatic examples of complex systems. Just think about the thousands of species interacting in complex ways within rich communities such as tropical rainforests or coral reefs. The most pressing questions ecologists face deal with concepts such as stability, resilience, thresholds and non-linearities which are at the core of the sciences of complexity. How robust are these cathedrals of biodiversity? At which rate will they disassemble as a consequence of global change. For example, one of the long-standing questions in ecology is the relationship between complexity and stability. In this contribution, I will present a brief review of some of the applications of the complexity sciences into the realm of ecological systems and discuss the implications for our understanding of ecosystems. Predicting the consequences of global change on biodiversity and the services it provides will need an interdisciplinary approach in which concepts from the sciences of the complexity may be very useful. Not only complexity sciences are important for ecology, but ecological research has also provided concepts and ideas to the science of complexity, for example in the context of deterministic chaos.

2 Introduction

Ecology is a relatively new science. It focusses on the relationships of species among themselves and with their environments. Because of the huge number of entities and their multiple interactions and feed-backs, the study of ecosystems is amenable to some macroscopic approach.

Although ecology has been an eminently descriptive science, important theoretical contributions were made almost from the beginning starting with the pioneering work by Lotka [68], Volterra [125], and Nicholson and Bailey [89]. These first contributions analyzed the dynamics of simple models describing two coupled populations such as a predator and its prey or two competing species. This early theoretical work defined the steady state solutions of these systems and their stability. The lessons from this exercise were to understand the possible dynamic outcomes from species interactions. For example, predators and their prey may get engaged in cycles. Some of these cycles were quite similar to cycles observed in nature such as the text book example of the Canadian Lynx and its main prey, the snowhsoe hare. The competition models, on the other hand, were used to understand under what circumstances two species will coexist. This type of models are usually more useful when they do not describe appropriately the reality pointing towards important missing variables. It is the case with the Nicholson-Bailey model [89] of a host parasitoid interaction, a type of specific predator-prey interaction in which an insect such as a wasp lies its eggs in, at, or near the

body of an arthropod such as a carterpillar. It is nature's own version of the celebrated movie Allien. Nicholson was fascinated by the coexistence of these insects whose abundances tend to oscillate in the field. However, the model was unstable and led to the extinction of one of the species. Thus, something else such as the consideration of space was needed as we will see below.

Models of one or a few species were later on replaced by other type of models representing entire communities. The dominant question revolved around the relationship between the complexity and stability of ecological communities [74]. Also, single population models were analyzed in the context of nonlinearities, as for example in relation to deterministic chaos [75]. Another emphasis was in stochastic models where ecologists explored how time to extinction scales with population size [43, 62, 31], and how species coexistence depends on fluctuating environments [23, 24]

Similarly, another extension of single-population, or two coupled population models was into the direction of addressing spatial degrees of freedom, that is, incorporating a spatial dimension and exploring how this new dimension made species coexistence easier.

Field ecologists, on the other hand, took other avenues but with similar goals. What regulates populations? What shapes the structure of communities? The first type of question emphasized the role of density-dependence versus external variables in explaining population change through time. The interest of this work is twofold since it may guide a biologically-informed pest

control as William Murdoch and colleagues have advocated [83, 84]. At the community level, the question was to understand the suite of mechanisms allowing the high levels of biodiversity that can be found in coral reefs and tropical rainforests. Joseph Connell, for example, analyzed the role of competitive interaction in structuring the marine intertidal [26] . In particular, he analyzed how patterns of recruitment, mortality and competition affected the distribution of barnacles [26]. More generally, he addressed how the high diversity in coral reefs and tropical forests is related to external perturbations in his famous intermediate disturbance hypothesis [27]. This states that the highest diversity levels are found neither in the absence of perturbations (competitive exclusion eliminates some species), nor with perturbations too frequent or intense (the bulk of species can not survive). Highest diversity levels are found at intermediate levels of perturbation.

Robert Paine emphasized the role of predation in controlling biodiversity in the intertidal [95]. His seminal work led to the concept of keystone species. He experimentally excluded the starfish in plots of the intertidal. The starfish is an important predator. It mainly preys a species of algae which is competitively superior, keeping a control on its abundance and allowing the coexistence of several algae species. When Paine removed the starfish, the competitively superior algae outcompeted the other algae species and the system become quite simplified. The predator had a strong interaction with its main prey and that had implications for the whole ecosystem. The importance of some species is much higher than what one would have predicted

based on their abundance. The keystone concept is extremely important in ecology. It has shown beyond any doubt the potential ecological impact of single species, and thus that we need to consider the roles of individual species in order to manage ecological communities [95].

What precedes is a very simplified and biased review of milestones in ecology and does not claim to be representative of the wonderful work that has been achieved in its century of history. It just tries to provide some general background on the ideas of diversity, complexity, non-linear dynamics and threshold behavior that will be illustrated in the following sections as examples of applications of the paradigm of complex systems to the problems of ecology and the preservation of natural resources in the face of human-induced perturbations. Next, I will explore this suite of studies and how they have shed light in our understanding of ecological processes.

3 Information Theory and Diversity

A great contribution in ecology was made from the perspectives of general systems. Ramon Margalef was pioneering the use of Information Theory as a way to describe ecological systems [70]. He was inspired by the work of Norbert Wiener, who introduced the concept of cybernetics [126, 4]. The key idea was to emphasize the feed-backs between components of the ecosystem as a way to understand the control of one system by another. A classic example of negative feed-bak is that between a predator and its prey. Predator and prey regulate each other's population as a thermostat would regulate a

room temperature. Margalef's book *Perspective in Theoretical Ecology* [71] was a classic in that regard. Margalef felt completely comfortable in the context of cybernetics because it perfectly described his view of ecology, a view defined as "the study of systems at a level in which individuals or whole organisms may be considered elements of interaction, either among themselves, or with a loosely organized environmental matrix" [70]. Information Theory was applied to ecology mainly as a way to characterize the diversity of an ecosystem measured as the number of different species and their relative abundances. Diversity would be maximum when each individual was from a different species, and minimum when all individuals were from the same species. Margalef used to talk about the museum and the agriculture field to refer to these two extreme cases.

In the context of the theory of information, an ecosystem is like a channel that transfers information. The amplitude of this channel is measured by the Shannon Entropy, which is a measure of disorder or uncertainty. In our context, let's say that we pick up randomly an individual. What is the uncertainty that this individual belongs to a specific species? Let's assume that an ecosystem has s different species, each one with an abundance $n_1, n_2, ...n_s$, so that the total number of individuals is $N = \sum_{i=1}^{s} n_i$. The probability that the randomly picked individual belongs to species i is then $p_i = n_i/N$, and one can define the diversity of the community as

$$H = -\sum_{i=1}^{s} p_i \ log_2 \ p_i \tag{1}$$

MacArthur [69] and many others advocated the use of this type of measures to describe diversity and many different uses of these indices have been done since then, for example in trophic studies of animal's diets, or in the quantification of energy flows in food webs [123].

4 Networks

Another significant contribution to a general system view of ecology was the concept of food webs, networks that represent who eats whom in ecological communities. These graphical representations of communities were first drawn by ecologists such as Lindenman and Odum [67, 90, 32]. Odum [90] used his engineering training to represent the interrelationships of ecological systems. As in the case of Margalef, he was emphasizing the interrelationships more than the nodes. He also had a broad and rich background that allowed him to think about ecosystems with fresh views. And he insisted in the concept of energy as one of the most important currencies in ecology. Odum used energy diagrams in the hope to see general patterns across systems regardless of taxonomic differences [118].

Food webs have constituted one of the classic subjects in ecology, with changing emphasis through the years. In the seventies and as a consequence of the seminal paper by Robert M. May [74], people started looking at food

web structure due to the evidence that structure greatly affects food web dynamics.

4.1 Stability and Complexity

May [74] used Gardner and Ashby's previous result to determine under what circumstances a random food web will be stable. This work was based on matrix algebra and was very successful at starting a rich research agenda. Roughly speaking, May was using Lotka-Volterra models with random interactions among species, and analyzed the probability of this model to be linearly stable. Given a certain connectance C measuring the fraction of non-zero interactions among species, May used previous results on random matrices to show that the system will be stable if

$$\alpha < SC^{-\frac{1}{2}}, \tag{2}$$

where S is the number of species and α is the average interaction strength among species. As noted from the previous inequality, the probability of a community to remain stable decreases as either the number of species or connections increases. This result essentially tells us that there are some constraints to randomly built communities to remain stable. Complexity begets instability, which contrasted with classical arguments by MacArthur, Elton and Margalef that suggested that complex ecosystems are more stable than simple ones. The question, thus, was to explore what properties of food webs counterbalance this tendency towards instability.

As a consequence of May's [74] paper, ecologists become interested in the modularity or compartmentalization of these ecological networks. The reason, at least in part, was the discussion at the end of that influential paper. May, after showing that complexity begets instability, performed some numerical experiments with non-random networks. He concluded his paper by noting that "*such examples suggest that our model multispecies communities, for a given average interaction strength and web connectance, will do better if the interactions tend to be arranged in "blocks" -again a feature observed in many natural ecosystems.*" Thus a whole research program was set on compartments. Part of the research focused on exploring the theoretical implications of compartments [98]; part was trying to explore whether real food webs are compartmentalized [99, 103, 58]. For a review on the studies on food webs see [25, 100, 117, 94]. This body of work emphasized invariant properties of food webs, their structure, the frequency distribution of interaction strengths, and simple models able to generate food webs with a similar structure as the observed in nature. I will not review this interesting literature in here; instead, I will emphasize the latest round of research in food webs that echoes similar work in complex networks. Recently, tools from the study of complex networks have been successfully applied to food webs. Food webs are now seen as another example of a complex network, with several papers comparing their structure with that shown by other types of networks such as the Internet, protein networks, or social networks (2].

4.2 Scaling in ecological networks

A first descriptor of network structure is the connectivity distribution, defined as the probability distribution of the number of interactions per node. The idea is to pick randomly a node in the network and represent the probability of this node interacting with one, two, ..., n other nodes. The relevance of this descriptor of network structure stems from two facts. First, from its relationship with early graph theory by Paul Erdös and Alfred Rényi [34] and recent build up models that generated a good correspondence between several models of network formation and their consequent connectivity distribution. Second, because the paper by Albert et al. [1] clearly related the shape of the connectivity correlation with the network robustness to error and attack. Albert et al. [1] found that the Internet has a connectivity distribution that follows a scale-free distribution defined by a power-law of the type:

$$p(k) \propto k^{-\gamma}, \tag{3}$$

where $p(k)$ is the probability of a node having k links and γ is a critical exponent. In a log-log plot, this relationship is defined by a straight line of slope $-\gamma$ for all the range of k values. That is, equation (3) is a relationship not defined on a particular scale. This would not be the case, for example, for an exponential distribution that has a specific scale, the average number of links per node [108].

Barabasi and Albert [6] , building on a previous result by Simon [110]

showed that a process of network build up where new nodes link preferentially with already well connected nodes (a type of "rich gets richer process) is a simple recipe to generate scale-free networks. On the contrary, a random model such as the classical random graph by Erdös and Rényi [34] generates distributions with Poisson distributions or exponential distributions if the number of nodes keeps growing. The important point is that in the latter case, the resulting network is much more homogeneous in the sense that all nodes have a similar number of interactions.

A randomly built network with connectivity distributions with thin tails, such as Erdös-Rény random graphs, are very fragile to the random deletion of nodes. After a certain fraction has been removed, the networks fragments. This fragmentation threshold will be revisited later on in the context of spatial processes, where space is represented as a regular (or irregular) network of points. Thus, random networks are very fragile [1]. On the other hand, scale-free networks are much more robust to the random deletion of nodes. One has to remove a high fraction before the network gets fragmented. The reason is that the few highly connected nodes (the hubs) play a major role in keeping the entire network together. Since these hubs are quite rare, it is very unlikely to remove them by chance. However, as shown by Albert et al. [1], these hubs are the Achilles' heel of the network. If one now starts removing the most connected nodes, the whole network collapses. Thus, scale-free networks are very robust to the random loss of nodes but very fragile to the loss of the hubs.

The work by Albert et al. inspired ecologists who turned to food webs in search of their connectivity distributions. Solé and Montoya [111] first analyzed a few food webs and found evidence for a scale-free distribution, while Camacho et al. [20] compared different distributions and found the best fit to be to an exponential distribution. Dunne et al. [30] generalized these previous results by using a broader data set and testing several functions. Their conclusion was that even when there were a few food webs described by fat tail distributions, the bulk of the food webs had tails following an exponential distribution.

Jordano et al. [53] extended the argument by focusing on a different type of ecological network, the one describing the mutually beneficial interactions between plants and their animal pollinators or seed dispersers (Fig. 1). These are two-mode networks with a much higher level of resolution than traditional food webs. While food webs have a high level of lumping so that a node contains several taxonomic species, mutualistic networks have a level of resolution almost always corresponding to a taxonomic species. These networks describe the coevolutionary process in species-rich communities [15]. This study analyzed 53 communities and concluded that in the bulk of cases, connectivity distribution for both plants and animals was best fitted by a truncated power law, a distribution of the following form:

$$p(k) \propto k^{-\gamma} e^{-k/k_c}. \tag{4}$$

The main difference in relation to equation (3) is the existence of a crit-

ical connectivity level k_c beyond which the connectivity distribution decays faster than expected for a power-law. These mutualistic networks are still very heterogeneous but not as heterogeneous as predicted for a scale-free distribution (Fig. 2) [53].

There are several non-exclusive factors that may account for the existence of these truncated power-law distributions. Jordano et al. [53] focused on what they termed *forbidden links*, that is, the existence of interactions that are not possible due to size or phenology uncoupling. For example, an insect can not pollinate a plant species if it is a migrant that arrives after the flowering period of the plant. Or a bird species will not disperse a tree species if their seeds are larger than the wide of the bird's beak. By combining analytic thinking and natural history, Jordano et al. [53] were able to account for a large fraction of the non-observed interactions in two well-studied communities.

Of course the fact that forbidden links exist and that their existence can lead to a truncation of an otherwise power-law does not exclude additional mechanisms. Forbidden links and similar mechanisms such as filtering information (i.e., a new node can sample only a subset of the network) constraint the preferential attachment mechanism. Other processes also lead to truncated power-law distributions without any constrain on such a process. For example, the same preferential attachment process taking place on a bipartite network leads to a truncated power-law distribution if there is any asymmetry between the two sets such as one set (e.g., plants) growing faster than

the other set (e.g., animals) [40, 41].

From the point of view of the robustness to species extinction of these mutualistic networks, the truncated power-law distribution confers more robustness than an exponential distribution to the random extinction of species but less dependence to the extinction of the hubs than for a power-law distribution.

4.3 Network structure: modules

The connectivity distribution is just a first description of network structure. In the general field of complex networks, scientist looked at deeper measures of network structure such as connectivity correlation or modularity. This was mainly analyzed for genetic networks and the Internet. For example, the connectivity correlation measures the average correlation between the number of links of a node and the average number of links of the nodes it interacts with. Maslov and Sneppen [73] found that both the internet and protein networks had a negative connectivity correlation, which means that hubs tend to interact with poorly connected nodes. This corresponds to an organization in compartments, which may buffer from the propagation of mutations or other perturbations [73]. Melián and Bascompte [78] applied this idea to food webs and found that they are more cohesive than the Internet or protein networks. Generalist species tend to interact among themselves. This may make these communities less robust to the propagation of a perturbation such as a contaminant, but more resistant to the extinction of a species. There is more

than a single way to be robust [78]. This description of food webs is complementary to a cohesive modular organization where several k-subwebs, that is, groups of species with at least k interactions among other species in the subweb, are linked to a densest central subweb which induces cohesion to the entire food web [79].

This work on the structure of food webs links to the early attempts to characterize compartments mentioned above [74, 99, 103]. In this regard, research on food webs [74, 98] pioneered the search for network structure that 30 years later would be so important in complex networks. The search for compartmentalization in food webs has not found too much evidence, partly because a lack of high quality data, partly because a lack of appropriate statistical tools to unambiguously define and characterize modules. More recently, Krause et al. [58] used software available to sociologists and found the strongest evidence of compartmentalization in three out of five food webs studied. In the context of the physics of complex networks, recent work has addressed the role of compartments in the structure of complex networks such as the world-wide air traffic [42]. Several algorithms to quantify modularity are now available. Olesen et al. [91] have used these algorithms to detect modularity in pollination networks. These modules are interpreted as the basic units of coevolution, that is, small groups of highly interacting plants and animals. The modularity analysis is useful in this context in showing the denser areas of the network. These denser areas have the potential to be coevolutionary hotspots or vortices [119].

Network structure such as modularity has also been looked for in the two-mode mutualistic networks. In this case, ecologists have used a concept from island biogeography, nestedness. In the mutualistic context, a matrix of plant-animal interactions is nested if specialists interact with species that form perfect subsets of the species generalists interact with (Fig. 3) [16]. This is a pervasive community organization that has been described for other ecological interaction such as those between cleaning fishes and their hosts [41], or parasites [60]. Nestedness implies a central core of interactions where generalist plants and generalist animals interact among themselves. This originates a dense core of interactions with a high level of redundancy and the possibility for the system to respond to perturbations. This is somehow in agreement with the cohesive organization of food webs found through the connectivity correlation and k-subweb distribution seen above. On the other hand, a nested mutualistic pattern implies an asymmetric pattern of specialization since specialists tend to interact with generalists. The latter tend to be more abundant and less fluctuating, and thus this community patterns confer mechanisms for the persistence of rare species [16]. Ecologists are now starting to explore the implications of these universal community patterns from the point of view of community responses to perturbations such as habitat loss [5, 37] or the invasions of foreign species [92, 80, 82, 19].

4.4 Weighted ecological networks

These heterogeneous, asymmetric network patterns in mutualistic networks are also observed in weighted networks. In this case, species strength, the weighted equivalent of species degree, grows faster than linear with species degree [7]. This pattern had been previously found for the world-wide airport network, but not for the scientific collaboration network [7]. The strength of highly connected species is even higher than expected based on their degree because specialists tend to interact exclusively with the most generalized species [16], and so depend completely on them. Thus, specialists contribute disproportionately to increase the overall strength of the generalists they depend upon. The nested structure of these mutualistic networks accounts for this pattern. The predominance of weak interactions and the asymmetry in pairwise interaction when a plant, for example, depends highly on an animal, tends to increase the conditions for the persistence and stability of species-rich communities as indicated by analytical results of a simple community model [8].

The role of weak interaction strengths on community stability has also been analyzed in studies of weighted food webs. This research agenda may be traced back to the seminal work by Robert Paine [95, 96] who in his classic experiments on the intertidal noted in the introduction, found that the strength of interactions between predators and their prey are defined by a few strong interactions in a matrix of weak interactions. This pattern has

then been observed over and over in other food webs and using other measures of interaction strength [123, 35, 103, 127, 14]. Simple dynamic models have shown that this frequency distribution of interaction strengths increases the stability of communities [77, 57]. However, the frequency distribution of interaction strength is only a first descriptor that does not tell us how these interaction strengths are combined in the basic components of the food web. Thus, Neutel et al. [88] found that weak interactions tend to be distributed in long loops. This avoidance of strong interactions in long loops induces the stability of the whole community [88]. Similarly, Bascompte et al. [14] found that that the co-occurrence of two strong interactions in a tri-trophic food chain occurs less often than expected by chance, and that in the few cases in which this occurs, it tends to be accompanied by strong omnivory (predator preying on two consecutive levels of the food chain) most often than expected by chance. These results have implications for the likelihood of trophic cascades, that is, changes in species abundance that transmit at least through two consecutive levels of a food chain. An example of a tropic cascade would be a decrease in sharks through overfishing, a subsequent increase in abundance of big fishes that constitute their prey, and a concomitant decrease in the abundance of smaller, herbivorous fishes the former prey on. Two strong interaction strengths have the potential to induce trophic cascades after the overfishing of top predators, but when accompanied by strong omnivory the magnitude of this cascade is severely reduced. Thus, in the light of the dynamic results of a biologically parametrized bionergetic model, one

can conclude that, other things being equal, the reduced frequency of two consecutive interaction strengths and their association to strong omnivory reduce the likelihood of trophic cascades [14]. However, this global pattern does not assure that the marine food web is buffered from the effects of overfishing, since overfishing does not affect randomly picked species but tends to focus on large, top predators. In the Caribbean food web, fishing selectively targets a biased sample of species belonging to upper trophic levels [86, 97]. These species, include ten heavily fished shark species from seven families that account for almost one-half of the strongly interacting food chains in the Caribbean food web [14]. The likelihood of trophic cascades after the overfishing of these predators is thus high. These cascades can contribute to the depletion of herbivorous fishes at the base of the chain such as parrotfishes that are important grazers of the algae. The reduction of these herbivorous fishes can accelerate the transition from corals to algae, an example of bistable steady state that will be considered later on in the context of ecosystem shifts as examples of phase transitions (see below).

First quantifications of interaction strength through energy fluxes was using information theory, the same framework we have described in the previous section in the context of species diversity [123]. New metrics to characterize weighted food webs build on this preliminary study [18].

4.5 Network motifs and trophic modules

A final parallelism between complex networks and ecological food webs has to do with network motifs, patterns of interconnections that are overrepresented in complex networks and that can be considered as the simple building blocks of complex networks [81]. Interestingly enough, there is a significant difference between research on network motifs and its equivalent research in ecology. The approach in complex networks is eminently structural, while that on their ecological counterpart is eminently dynamical. For example, the first papers on network motifs quantified their representation in entire networks and compared their frequency with that predicted by appropriate null models. Only later on there were some studies exploring the dynamics of these different motifs [101]. On the other hand, ecology has been studying the dynamics of simple trophic modules such a tri-trophic food chains without looking at how frequent are these simple modules in entire food webs [13]. What it remains to be done now is to scale-up from these isolated modules to the entire food web.

5 Complex Dynamics

Let us now move from structural complexity to dynamical complexity. There is a strong relationship between ecology and complexity sciences in the context of population dynamics. As a matter of fact, one of the seminal contributions to deterministic chaos came from theoretical ecology. Once more, the

great talent of Robert May was behind this contribution [79]. May was looking at one of the simplest models one could think of in theoretical ecology. It describes the dynamics of populations with non-overlapping generations. Let's assume that the density of insects in a generation t is N_t. Let's first normalize this value by dividing it by the highest density ever observed N_{max} so that $x_t = N_t/N_{max}$. If we imagine a deterministic model with density dependence, one can write what the density of insects at the next generation will be

$$x_{t+1} = \mu x_t(1 - x_t), \tag{5}$$

where μ represents the population rate of increase. Robert May analyzed the temporal dynamics of system (5) as he was increasing the growth rate μ. For very low values, the population goes extinct. When $\mu > 1$ the population reaches a steady state. If μ is further increased, at $\mu >3$ the steady state becomes unstable and a cycle of period two becomes stable. For even higher μ-values, there are other period doubling bifurcations and so the population oscillates with cycles of higher frequency. Finally, when μ reaches a critical value the dynamics never repeats itself, the system shows deterministic chaos [79].

The finding of this period doubling route to chaos in an ecological model opened a research agenda that found that this scenario has universal properties, e.g., the relationship between the successive critical μ_k values at which a new bifurcation k appears are independent of the model. More than that,

even in experimental systems one could observe the same universal laws [37]. Specifically, Feigenbaum showed that for a large enough μ-value, the following relationship takes place:

$$\delta = \lim_{k \to \infty} \frac{\mu_k - \mu_{k-1}}{\mu_{k+1} - \mu_k} = 4.6692..., \tag{6}$$

The co-discovery of deterministic chaos in the logistic equation (together with parallel work in meteorology and mathematics) had a huge importance, not only in the field of ecology, but beyond. It is one of the few examples in which the flow of ideas has gone from ecology to physics. Since this important discovery, a rich research program of research in ecology revolved around the role of deterministic chaos in ecological systems, both theoretically [76] as well as empirically [106, 51].

5.1 Chaos in the real world

William Schaffer and Mark Kot [106] were among the pioneers in looking for deterministic chaos in real ecological systems such as the cycles of the Canadian lynx or the monthly records of measles in big cities. Ecology was facing the possibility that complex temporal series were not the result of hundreds of stochastic variables, but of a few variables in deterministic, yet non-linear dynamical systems [52]. This is not just a technical issue. If complex dynamics in the populations of diseases or pests were deterministic we could understand the underlying rules. However, the evidence for chaos has been more evasive due to the shortness of temporal series and their high

amounts of noise.

Arguably, the first serious attempt to quantify chaos in nature was the paper by Hassell et al. [47], who analyzed the temporal series of 28 arthropod insects from both the lab and the field. Detecting chaos depends very much on the way to attempt so, and ecologists have been very imaginative in their search for chaos in a noisy world. In this first study, Hassell et al. fitted their temporal series to a previously studied non-linear population model. Twenty-six populations had temporal series which best fit model parameters within the parameter region corresponding to steady states, and only one example corresponded to the region of deterministic chaos. This was thought to be little empirical support for chaos to begin with.

Schaffer and Kott [106] used a different approach and different data sets, and their work supported the notion that chaos may be common in ecology. They used the same techniques physicists were using, such as attractor reconstruction and estimation of its fractal dimension. Several time series such as the Canadian lynx had attractors reminiscent of the strange attractors that are the hallmark of deterministic chaos. Similar results were obtained for the measles records in Baltimore [106, 3].

Sugihara and May [116] used non-linear forecasting techniques to distinguish deterministic chaos from noise (both correlated and uncorrelated). This clever approach is based on dividing the temporal series in two halves and using the first half as a source of known data, and considering the second half as the unknown future. The correlation coefficient between predicted and ob-

served values is plotted versus prediction time. Deterministic systems show an exponential decay in correlation, while this is constant for noisy systems. Ellner and Turchin [32] used non-linear techniques to estimate the largest Lyapunov exponent, i.e., the parameter telling at which rate two nearby trajectories in the phase space will diverge. Their strategy to reduce the high levels of noise present in the original time series was to first estimate the map that best fits their temporal series, and then using it to calculate the Lyapunov exponent from the dynamics of the map. Tilman and Wedin [120] build a Poincaré map by plotting the biomass of annual plants one year versus the same biomass the next year. The slope of this map for a vegetation model previously used dictates whether the system is or not chaotic. In summary, there was a serious effort to look for chaos in real ecosystems by using a broad spectrum of techniques. There were evidences for chaos but also evidences against its presence. This line of research is almost extinguished, but a recent paper by Sibly et al. [109] touched on it by estimating return rates after a perturbation for a very large number of temporal series of groups of mammals, birds, fish, and insects. They found that in the bulk of cases the return rates were quite below the threshold for chaos, which corresponds to stable populations. However, there is a clear case for the potential of chaos in population dynamics, a beautiful example that comes from an interaction between analytical and lab work.

Costantino and colleagues [28, 29] combined an experimental setting where a population of the flour beetle *Tribolium* was growing in milk bot-

tles, and a population dynamic model that, although simple, incorporated the basic dynamics of the species life cycle. This was a discrete time model that described the three phases of the beetle life cycle, namely feeding larvae, non-feeding larvae, and adults. Cannibalism is very common in this species and mathematically induces a strong nonlinear term that is partly responsible for the presence of deterministic chaos. This team first proceeded by parametrizing their model with the temporal data they obtained in the lab. From the experimental point of view, they manipulated the recruitment rate into the adult stage by adding or removing adults at the time of the census. As this recruitment rate was increased, there was a sequence of period-doubling route to chaos shown both by their lab census as well as by their model with the adequate parameter values.

In sum, maybe chaos is not common in nature, but nature certainly has the potential to show chaos.

6 Spatiotemporal Dynamics

Deterministic chaos was perhaps the first pedagogical example of the potential of non-linear dynamics in ecology. The lesson was that other dynamical behaviors beyond steady states and cycles are compatible with a deterministic, density-dependent model. The next finding of the potential of non-linear dynamics to generate complex phenomena was provided by the study of dynamic systems extended in space. Imagine a discrete lattice of sites simulating the patchy distribution of some available habitat. Within

each one of these habitat patches a local population can be described by a dynamic model such as the logistic map. However, we allow now for the fact that a fraction of the individuals born in a patch disperse to neighboring sites. The resulting spatiotemporal dynamics can be described by the coupled map lattice (CML), a dynamical system with discrete time, discrete space and continuous state, first used by the Japanese physicist Kunihiko Kaneko working in problems of diffusion and spatiotemporal chaos [54, 55]. This approach allows to easily study the combined action of two processes: local dynamics (described by an appropriate *map* or discrete time model such as the logistic equation (5), and the coupling through dispersal of these local maps. A CML can be written in the following way:

$$x_{t+1}(i) = (1 - D)F\{x_t(i)\} + \frac{D}{k}\sum_{j=1}^{k} F\{x_t(j)\}, \tag{7}$$

where $x_t(i)$ is the density of population at site i and time t, D is the fraction of individuals leaving its patch and k is a certain neighborhood around a local patch where individuals can move to. Coupled map lattices such as (7) have been extensively used in ecology [10 112]. For example, coupled map lattices have shown how dispersal may affect the temporal dynamics [49], and the length of the transients [50]. Particularly relevant is the finding of spatial self-organizing patterns such as spiral waves in the abundance of populations [46, 113, 48]. This phenomenon is qualitatively similar to the one found for excitable media where symmetry breaking takes place around a pacemaker

[85]. From the point of view of ecology this suggests that simple rules can create long-range spatial patterns. Similar spatial models belong to the class of interacting particle systems, where not only space and time are discrete, but also the state of a cell is on one of a few discrete values. As opposed to CMLs, the latter are stochastic models for which there is a rich body of mathematical work addressing, among others, how spatial pattern arises in ecology [31]

Coupled map lattices are useful to link patterns at different spatial scales. The problem of pattern and scale is at the core of ecology [64]. For example, one can describe the population dynamics at a lattice site. In the case of a chaotic map, this dynamics will be quite unstable, with strong fluctuations. This unstable character was one of the arguments by which some field ecologists argued that chaos would not be common in nature [17]. If populations oscillate so heavily, at some point population density will be low enough for stochastic events to lead the population extinct. However we can now see the same unstable dynamics from a larger spatial scale, let's say that we plot the total abundance in 2x2 lattice sites, 4x4 lattice sites, and so on. How unstable the chaotic dynamics will look like? Surprisingly, the dynamics will now appear very constant. Solé and Bascompte [10, 112] coined the term *chaotic stability* to refer to the fact that chaos and its instability at a local scale can induce a strong stability at a global scale. Thus, the criticism of chaos based on its instability does not apply when space is considered.

One way to understand the previous result is remembering the strong de-

pendence on initial conditions of a chaotic system. Because of that, two nearby local populations will start to oscillate out of phase, and so ups and downs will soon cancel each other. Technically, this can be analytically proved following reference [105]. These authors found a relationship between the largest Lyapunov exponent and the spatial coherence length. The coherence length describes how far away two points oscillate in a correlated way. As a matter of fact, the inverse Lyapunov exponent can be regarded as a correlation time, i.e., the time horizon beyond which two initial trajectories fluctuate totally independent from each other. In the vicinity of the onset of chaos, the following relationship between the largest Lyapunov exponent (λ) and the spatial coherence length (ξ) holds: $\xi \approx \lambda^{-1}$. Thus, the more chaotic a system is, the faster spatial correlation decays with distance. An application of this idea in ecology was proposed by [11], providing a clear mechanism for an early suggestion by [120] on the difficulty to detect chaos at larger spatial scales even when present at local scales.

Another interesting application of coupled map lattices is to the problem of pattern formation, which is a celebrated one in several fields such as developmental biology and excitable media [85]. In the context of ecology, pattern formation in space is related to the problem of species coexistence. This is another example when introducing spatial degrees of freedom changes entirely our picture of ecological systems. At the beginning of this contribution I already mentioned that Lotka and Volterra had derived a mathematical model for two competing species. The lesson from that model was that the coex-

istence of the two species is only compatible with low values of interspecific competition. One interesting avenue has been analyzing the mathematical conditions under which species coexist under different environmental fluctuations [23, 24]. Another aspect has been considering the spatial component. If one considers the spatial extension of a competitive model, local exclusion is compatible with global coexistence if stochasticity plays a role in the dynamics. From a spatially homogeneous setting where both species were initially present, one ends up with clusters of patches where species one is the survivor and alternative clusters where the second species wins [114]. These steady state spatial patterns are equivalent to Turing patterns in models of development.

An even more striking example of spatial self-organization is the existence of spiral waves such as the ones observed in excitable media as some chemical reactions or electric activity in the heart [38, 85]. If one extends the host parasitoid model by Nicholson and Bailey into a coupled map lattice, one can observe the spontaneous emergence of traveling waves in the density of one of the species (Fig. 4) [46, 115, 113]. This is relevant from several points of view. From the point of view of complex systems, this shows how the interplay between local non-linear dynamics and short-range dispersal can generate large scale self-organized spatial patterns as first shown by the great mathematician Alan Turing [121, 64]. This opens a new way to interpret large scale patterns in ecology, traditionally adduced to reflect environmental causes [14]. Interestingly, these spiral waves are related to the persistence

of interacting species: once more, despite the local instability, the system is globally stable and all species coexist more easily than predicted by non-spatial models.

Coupled models have also shown how dynamics can be affected by dispersal. For example, reaction-diffusion models of population dynamics have illustrated the dispersal-induced route to chaos, that is, the change in the type of dynamics from steady states to cycles and to chaos as the dispersal rate is increased [59, 93]. Similarly, coupled map lattices have shown how the transient time in non-spatial models becomes now extremely large [50], which had also been noted by Kaneko from a physical perspective. This has important implications in ecology. We implicitly assume that the steady state is the relevant dynamics, but if transients are as long as thousands of years, transient dynamics may be much more relevant for ecology than long-term steady states [50].

As for the case of deterministic chaos, a myriad of papers looked for these self-organizing patterns in nature, and good evidence for pattern formation come from examples of rodents in northern Europe [104], host-parasitoid interactions [72], and outbreaks of the moth *Zeiraphera diniana* in the Alps [19]. Once more, theory was ahead and lead field ecologists to search for examples of complexity in real nature. This was expanding our horizons and moving from a classical view of ecosystems where all complex processes were associated to external variables, to another scenario where internal processes were able to account for much of the complexity observed in real nature.

7 Thresholds

One important application of the sciences of complexity is the concept of phase transition from statistical mechanics. This is very important because in ecology we are used to think in terms of linear relationships between a cause and its effects. Oftentimes, as we tune a parameter we find the occurrence of a critical point in which a sudden qualitative change takes place. A previously stable solution becomes unstable and two new stable solutions emerge, as we have seen in the period-doubling route to chaos. A symmetry-breaking process takes place and the system choses one of the two possible solutions. A mechanical analogy would be a ball rolling on a surface with two minima. This describes the dynamics of a phase transition.

The paradigmatic example of a second-order phase transition in physics is the Ising model. This model describes the behavior of a set of magnets on a square lattice of length side N. The state of each lattice site i at time t is defined by the spin $S_t(i)$. Each spin can be in the states upwards (1) or downwards (-1) and interacts with its four nearest neighbors to minimize energy, that is, to have parallel alignment. The global magnetization is $M = \sum_i S_i$, and the idea is to plot this measure as a function of the temperature. For high temperatures, noise dominates, and the distribution of spins is random, i.e., $M = 0$. At very low temperatures, the system is ordered and all spins point towards the same direction (either upwards or downwards). M becomes maximum. As we progressively decrease the temperature, a sud-

den transition takes place at a critical temperature T_c. The magnetization per spin $m = M/N$ behaves close to T_c (for $T < T_c$) as $m \approx |\tau|^{\alpha}$ where $\tau = (T - T_c)/T_c$ [107].

A relevant parameter to characterize spatially distributed systems is the correlation length ξ. For $T > T_c$ we already said the system is random and correlation lengths are small. Close to T_c, ξ scales as $\xi \approx |\tau|^{-\nu}$, ν being another critical exponent. Below the critical point, the model exhibits long-range order. Clusters exist on every length scale. That is, the system is scale-free. The correlation length ν, the size of the maximum cluster, and the variance in sizes diverges to infinity as we approach the critical point.

Percolation theory has had a nice application as a null model in landscape ecology [122]. A useful example is its application to the problem of habitat fragmentation. This is an extraordinarily complex problem due to the accelerating rates of habitat destruction everywhere and the well-known fact that habitat transformation is the number one cause of biodiversity decline. Imagine a spatial lattice as the one described above. A direct application of percolation consists in envisioning a situation in which each site is originally pristine, i.e., occupied by vegetation, and one proceeds by destroying an increasing fraction of randomly placed sites. As for the Ising example, the size of the largest patch starts declining smoothly at the beginning. A new destruction event just reduces the size of the single large patch by one site. But close to the percolation threshold, an additional destruction implies that the previously continuous cluster breaks down in small pieces. To separate

the effects of habitat loss from those of habitat fragmentation, one can use the following order parameter [9]:

$$\Omega = \frac{S_{max}}{\sum_{k=1}^{N} \Theta(k)}, \tag{8}$$

where S_{max} is the size of the largest cluster, and $\Theta(k)$ is one if site k is available, and zero if it is destroyed. As can be easily seen, when all available sites belong to the same cluster, the previous equation is one. From a biological point of view, it means that we are only facing habitat loss. However, when habitat loss induces habitat fragmentation, the value of the order parameter drops suddenly. This is because we have now several disjoint clusters of vegetation, and thus only a small fraction of the available sites belong to the largest cluster. Interestingly enough, the order parameter drops really fast near the percolation threshold, so its value is one below a critical level of habitat destruction, and becomes almost zero after that threshold.

7.1 Extinction thresholds

The above non-linear changes in landscape structure as more habitat is destroyed has implications for the persistence of a species inhabiting such a landscape. Species inhabiting heterogeneous landscapes living in a dynamical balance between local extinctions and recolonizations from neighborhood patches are called metapopulations [66, 45]. If we plot the regional abundance of a metapopulation (i.e., the fraction of sites occupied) versus the fraction of sites destroyed, one observes the presence of an extinction thresh-

old defined as a critical destruction value at which the metapopulation goes extinct despite a fraction of the habitat is still available [61]. In spatially explicit systems with local dispersal, the rate at which a metapopulation's regional abundance decreases is faster than in the case of spatially implicit models. That is, the effects of habitat loss are higher as more habitat has already been destroyed [9]. The reason has to do with the previously reported non-linear changes in the landscape. Essentially thus, habitat destruction models are equivalent to models of phase transitions in statistical mechanics. This theory has served to better understand the consequences of habitat destruction on metapopulations. It has been very pedagogical in suggesting how changes in ecological systems are not smooth, but rather non-linear.

The presence of extinction thresholds in metacommunity dynamics is equivalent to the eradication thresholds in epidemiological models. Nee [87] already noted the equivalence between these two types of models and their critical points. These critical points can be simplified to expressions where species-specific parameters such as colonization or transmission rates cancel out. Eradication thresholds can be phrased as the points at which the destructive process reaches the amount of resource used when all the resource is available. For example, consider the following metapopulation model originally proposed by Levins [66]:

$$\frac{dv}{dt} = cv(1 - v - D) - ev. \tag{9}$$

The previous equation assumes an infinite number of habitat sites and de-

scribes the temporal dynamics in the fraction of sites occupied by a metapopulation (v). It contains a positive term describing the increase in occupied sites due to the colonization of empty sites. c is the species-specific colonization rate, and D is the fraction of sites permanently destroyed. The second term in equation (9) refers to the loss of previously occupied sites due to local extinction, e being the extinction rate. Note that the previous model can also be used as a toy model of an infectious disease, in which case v would be the fraction of hosts infected, c would be the transmission rate, D would be the fraction of hosts vaccinated and e would be the clearance rate. Model (9) has a positive steady state as long as the fraction of sites destroyed (hosts vaccinated) is lower than the threshold $D_c = 1 - e/c$. As noted by Nee [87], this threshold is equivalent to the steady state in the absence of destruction: $v^* = 1 - e/c$. Thus, one can predict D_c without knowing the parameters c and e by measuring the amount of habitat occupied when all habitat is pristine. This simple rule was coined as the Levins rule (Hanski et al. 1996). In epidemiological models, the infectious disease disappears when the fraction of hosts vaccinated is equal to the fraction of non-infected hosts when all hosts are susceptible [87, 12]. Similar ideas can be applied to the dynamics of transposable elements, a type of intragenomic parasites [12].

Stochastic spatial models such as the contact process have allowed to derive mathematical conditions under which a species will persist or die out with almost certainty, that is, similar thresholds for species persistence [31]. In these review we have encountered both spatially explicit models such as

the CMLs and the interacting particle system, as well as spatially implicit models such as Model (9). There are analytical approaches such as moment-closure that allow to bridge between these two extremes [65].

7.2 Ecosystem shifts

Thresholds such as the one here illustrated for the case of habitat loss are common in ecology. One can find several examples in which a variable is smoothly changed with no apparent consequence in the macroscopic properties of the system until a threshold in which an abrupt transition in the state of the system takes place. These are known as ecosystem shifts [107, 112]. One classical example of an ecosystem showing two alternative steady states is that provided by shallow lakes [22, 107]. There are documented examples were a lake has shifted between an initial state characterized by clear water and submerged vegetation to a state characterized by turbulent water, a high concentration of phytoplancton, and an absence of submerged vegetation. This lack of vegetation is associated with a reduction in diversity, since several species of fishes and other taxa use vegetation as food and refugia [107]. This transition in shallow lakes occurs as a consequence of human-induced eutrophication, and constitutes a global problem affecting also small seas such as the Baltic. The tuning parameter in this example would be the amount of fertilizers dumped into the lake. As one starts increasing this parameter nothing seems to occur in a while. Until the critical point is reached and the new state suddenly takes place. Once more, there is

no apparent correlation between the last push and its amplified consequence. Shallow lakes show a profound hysteresis in response to nutrient load [107]. This means that the system is irreversible, and that environmental actions to recover the pristine state may be costly. Now one needs to almost clean the lake completely to revert the change to the pristine state.

The case of a lake is by no means the only example. Other examples involve the transitions from corals to macroalgae, or from herbaceous vegetation to bare desert. In the first case, extensive areas of coral reef have been replaced by a system dominated by algae. Corals hosts countless numbers of other species. Currently, ecologists have started documenting these transitions and looked for their explanations. Several non-exclusive explanations involve increased nutrient loading and overfishing that have decreased the abundance of herbivorous fishes, thus freeing algae from their control and allowing them to take over and replace corals [52]. Overfishing of sharks may have also contributed to the depletion of herbivorous fishes through trophic cascades [14].

The transition from a vegetated state to a desert one is also one of concern. Vegetated and desert seem to be two alternative stable states. This has example has further implications in the context of global change and can feed-back into further increases of temperature without the layer of vegetation. Knowing that these transitions are irreversible due to the hysteresis cycle is worrisome as has also profound implications in the context of human migrations in search of available water.

8 Future Directions

The previous cases of ecosystem shifts suggest the role for non-linearities in conservation biology. The take home message is that we can not think anymore in linear terms. There is not necessarily a proportional relationship between cause and consequence. This calls for caution when assessing the consequences of global change and other types of human-induced perturbations. For example, the consequences of habitat destruction may even be worse than expected and further destruction values may cause the system to cross a threshold where extinctions may take place at a much higher rate. The existence of ecosystem shifts suggests that ecological systems may behave in qualitatively similar terms than other simpler physical systems. This is good news in the sense of being able to use a well-developed theoretical framework to make predictions of ecological systems. Near the critical points the system's macroscopic properties may be described by simple models [112].

On the other hand, due to the abrupt changes that take place in the critical points, it is very important to develop early indicators of the proximity of a system to such thresholds. For example, Kleinen et al. [56] analyzed changes in the power spectrum of temporal series and concluded that there is a reddening of the signal in the vicinity of the critical point. Similarly, there is increasing evidence that a clear early-warning signal of an ecosystem shift is an increase in the variance of the temporal series [124, 21]. Further studies will be very useful in developing new and easy to measure early-warning

signs. This may be very important in predicting major shifts in the state of ecosystems and the services they provide.

To sum up, ecological systems are wonderful examples of complex systems with multiple states, phase transitions, and non-linear dynamics. They provide opportunities to further apply concepts and tools from the physics of complex systems. And in the face of the multiple risks from global change, there is an urgent need to do so.

Funding was provided by the European Heads of Research Councils, the European Science Foundation, and the EC Sixth Framework Programme through a EURYI (European Young Investigator) Award.

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10 Figure Captions

Fig. 1. The mutually beneficial interactions between plants and their animal pollinators (picture) and seed dispersers have played a major role in the generation of Earths' Biodiversity. Picture courtesy of Mark Chappell.

Fig. 2. The mutualistic interactions such as the one depicted in Figure 1 form complex networks of species interdependence. The architecture of these networks greatly affect their robustness to the extinction of one of the species. The picture represents a plant-pollinator network in the Arctic. Plants and insects are represented as green and yellow nodes, respectively.

Fig. 3. The nested assembly of mutualistic networks. Two-mode Interacting networks are represented as a matrix with plants in rows and animals in columns. A square indicates that the plant in this row and the animal in this column interact. Panels a, b and c represents a totally nested, random and real network. The line in c represents the isocline of perfect nestedness. Modified from Bascompte et al (2003).

Fig. 4. Spiral waves in a coupled map lattice model of interacting populations. The figure corresponds to an iteration and each lattice size codes the abundance of hosts in a host-parasitoid system. These self-organizing spatial patterns are very much related to the persistence of populations.